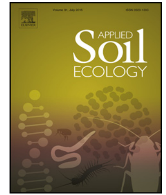
Applied Soil Ecology 108 (2016) 228–237

Contents lists available at ScienceDirect

Applied Soil Ecology

journal homepage: www.elsevier.com/locate/apsoil



Aluminum tolerance of wheat cultivars and relation to arbuscular mycorrhizal colonization in a non-limed and limed Andisol

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ARTICLE INFO

Article history:
Received 10 December 2015
Received in revised form 1 August 2016
Accepted 18 August 2016
Available online xxx

Keywords:
Aluminum resistance
Glomalin related soil protein
Genetic variation
Nutrient acquisition

ABSTRACT

Wheat (*Triticum aestivum* L.) cultivars vary extensively in their response to acidic soils. In southern Chile, wheat genotypes have been selected for growth on acidic Andisols where high concentrations of phytotoxic aluminum (Al) limit plant growth. Previous work indicates that arbuscular mycorrhizal (AM) fungi play an important role protecting plant roots against the deleterious effects of Al. To understand interactions between AM fungi and cultivar Al phytotoxicity, six locally used wheat cultivars ('Bakan', 'Crac', 'Invento', 'Maxi', 'Otto', and 'Porfiado') were cultivated in a non-limed and limed Andisol (74 and 5% Al saturation, respectively). Plant harvests were carried out at two phonological stages: tillering (60 days after sowing, DAS) and physiological maturity (150 DAS). Plant growth was limited on non-limed soil, but varied by cultivar. Among the cultivars, 'Porfiado' and 'Crac' exhibited growth traits consistently associated with acidic soil resistance, including greater biomass and root length and higher P/Al and Ca/Al ratios in plants grown in non-limed soil. Wheat growth was positively correlated with AM colonized root length and Al bound to glomalin related soil protein (Al-GRSP). In addition, root Al concentration was negatively correlated with colonized root length and Al-GRSP across all wheat cultivars grown under high Al saturation. The significantly better performance of wheat cultivars and their association with AM fungal traits on non-limed soils indicates that indigenous AM fungal populations in acidic soils may contribute to Al tolerance of some wheat cultivars when growing at high Al levels.

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1. Introduction

Aluminum (Al) ions in the soil solution represent one of the main limiting factors for plant growth on acidic soils (Ritchie, 1994; Kochian et al., 2004; Fageria and Baligar, 2007; Ryan et al., 2011), inducing diverse physiological perturbations that ultimately reduce root and shoot growth and yield (Delhaize and Ryan, 1995; Ma et al., 2001; Kochian et al., 2005; Panda and Matsumoto, 2007; Inostroza-Blancheteau et al., 2012). In addition, the excess of protons (H^+) and deficiencies of essential nutrients such as phosphorus (P), calcium (Ca), magnesium (Mg), and molybdenum (Mo) are also important stress factors in plants growing in acidic soils (Marschner, 1995; Driscoll et al., 2001; Tang and Rengel, 2003). These conditions are prevalent throughout the tropics (Fageria and Baligar, 2007), in temperate regions (St. Clair et al., 2008), and also in volcanic soils from southern Chile (Sadzawka, 2006; Mora et al., 2006).

To decrease the deleterious effects of soil Al on plant growth, agronomical management practices include lime and P fertilizer application (Havlin et al., 2004) and/or the use of Al-tolerant genotypes of crop plants (Gourley et al., 1993; Mora et al., 2002). Whereas lime and P fertilizer reduce soil Al^{3+} activity, and incur significant financial costs, the selection of Al-tolerant lines may similarly reduce Al^{3+} activity with lower agronomic inputs for production because the processes detoxifying Al are plant-related traits (Ryan et al., 2011). Aluminum resistance is often associated with genotypes expressing Al-triggered exudation of organic acids, which function to chelate and detoxify Al in the rhizosphere (Kochian et al., 2004, 2005). At the same time, these changes in rhizosphere chemistry lead to increases in P and Ca acquisition by plants, increasing growth on acidic soils (Zheng et al., 2005; Delhaize et al., 2009).

Seguel et al. (2013) recently reviewed the roles played by arbuscular mycorrhizal (AM) fungi in protecting the roots against Al toxicity. While there exists a wide range of benefit accrued by host plants, general reductions in tissue Al and increases in tissue P and Ca concentrations and water uptake by mycorrhizal plants compared to non mycorrhizal plants suggest that, as with root

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http://dx.doi.org/10.1016/j.apsoil.2016.08.014
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exudation, exudation of organic acids or the production of novel mycorrhizal compounds may alter Al chemistry in soils (Lux and Cumming, 2001; Cumming and Ning, 2003). In support of these patterns, Klugh and Cumming (2007) and Klugh-Stewart and Cumming (2009) concluded that some AM fungi strains confer higher Al tolerance to plants through increased organic acid exudation, which decreases the concentration of free Al^{3+} in the root environment.

In addition, other studies have shown that glomalin, a glycoprotein produced by AM fungi and released to the soil in high amounts (Wright and Upadhyaya 1996, 1998; Gadkar and Rillig, 2006), may immobilize large quantities of toxic metals (Gonzalez-Chávez et al., 2004; Cornejo et al., 2008; Vodnik et al., 2008; Aguilera et al., 2011; Gil-Cardeza et al., 2014; Seguel et al., 2015). Glomalin related soil protein (GRSP, as it is quantified) represents a significant fraction of the soil pool of protein due to its persistence, contributing significantly to the binding of soil particles, stability of soil aggregates, and carbon sequestration (Rillig and Mummey, 2006; Bedini et al., 2007; Curaqueo et al., 2011). GRSP may have the ability to contribute to plant Al resistance due to its Al-complexing capacity (Aguilera et al., 2011; Seguel et al., 2015). This binding would represent an important external mechanism to reduce Al toxicity in mycorrhizal plants growing on acidic soils where high exchangeable Al levels constrain agricultural production (Seguel et al., 2013).

Variation among AM fungi in response to Al or capacity to confer acidic soil resistance to host plants may be the consequence of substantial genetic variation among and within AM fungal species (Bever et al., 2001), which may provide different benefits depending on the edaphic environments (Vosatka et al., 1999; Kelly et al., 2005; Pigna et al., 2014; Barea, 2015). In the case of acidic soils with high Al levels, there is a wide variation amongst AM fungi ecotypes to acid conditions evidenced by differences in spore germination, hyphal growth rate, root colonization percentage, and diversity indices (Klugh and Cumming, 2007; Aguilera et al., 2014). Furthermore, early colonization can be an important factor in Al tolerance and, consequently, beneficial against Al toxicity (Seguel et al., 2012, 2016).

The objective of this study was to assess the innate Al resistance and AM fungal contribution to Al resistance of six Chilean wheat cultivars by using a native non-limed Andisol with high Al saturation and a lime treatment of this soil. We assessed root colonization, spore production, and the production of GRSP, and Al-GRSP as well as growth and plant nutrition measures. We hypothesized that cultivars that support greater AM colonization will foster reductions in Al exposure and reduce Al impacts on nutrient acquisition and growth on the non amended Andisol.

2. Materials and methods

2.1. Soil, plants and growing conditions

The soil utilized was an Andisol (Gorbea series, medial, mesic, Typic Dystrandept) collected to 20 cm depth. The soil was air-dried, sieved through a 5 mm mesh, amended or not with commercial lime (91% of $CaCO_3$, 5% of $Ca(OH)_2$ and 2% of S and Mg) at the equivalent rate of 4 ton lime ha^{-1}, and incubated for two weeks in the greenhouse. Some characteristics of the non-limed and limed soil are described in Supplementary data (SD1).

Seeds of six Chilean cultivars of *Triticum aestivum* L., 'Bakan', 'Crac', 'Invento', 'Maxi', 'Otto' and 'Porfiado' (von Baer, 2007), were surface-sterilized with 2% Cloramin-T solution for 3 min and rinsed thoroughly with H_2O. Fifty seeds per cultivar were germinated between wet tissue paper and six seedlings per cultivar were transplanted 7 days after seed germination separately into 1 L pots filled with 800 g of non-limed or limed soil. After thinning, three plants were grown under greenhouse conditions with temperatures ranging from 25 ± 3 °C day to 15 ± 3 °C night, a 16/8 h light/dark photoperiod, and a relative humidity of 80–90%. The plants were irrigated manually with distilled water as needed during the experiment. Nitrogen (N) was supplied in two portions, at establishment (30% total N) and at 6 wk of cultivation (70% total N), supplied as $NaNO_3$ to an equivalent amount of 0.113 g N kg^{-1} soil. Phosphorus was supplied to 0.016 g P kg^{-1} soil as NaH_2PO_4 and potassium (K) was supplied to 0.063 g K kg^{-1} soil as KCl, respectively before establishment. All nutrients were supplied as solutions. Pots were harvested at two growth stages, at tillering (60 days after sowing, DAS) and physiological maturity (150 DAS). At each harvest, plant and fungal variables were measured as is described below.

2.2. Measurements

At both harvests, the plants were separated into roots and shoots, and a portion of the root was separated, gently washed free of soil and AM colonization was measured. Fresh root fragments (1-cm length) were collected from throughout the root zone, stained with trypan blue, and cleared in 10% KOH following the method of Phillips and Hayman (1970). Mycorrhizal colonization was determined by the grid-line intersect method (Giovanetti and Mosse, 1980). Total and colonized root lengths were calculated by Tennant (1975) and Brundrett et al. (1994).

The remaining shoot and root tissues were dried at 65 °C in a forced-air oven for 48 h and weighed. Shoot and root tissues obtained from the final harvest were crushed, ground, ashed in a furnace at 550 °C, and dissolved in $H_2O/HCl/HNO_3$ (8/1/1 v/v/v). Phosphorus in tissue digests was determined colorimetrically using the vanado-molybdate method (Hanson, 1950) and Al, Ca, and Mg were determined by AAS.

Soil fungal parameters, including spore density, total hyphal length and GRSP, were determined in soils before sowing and at final harvest (150 DAS). Arbuscular mycorrhizal spores were determined according Sieverding (1991) and total hyphal length was measured according Rubio et al. (2003) and quantified by the grid-line intersection method (Newman, 1966). Total GRSP was determined according to the method described by Wright and Upadhyaya (1998) with minor modifications optimized for our volcanic soils as follow. Total GRSP was extracted from 1 g of soil with 8 mL of 50 mM Na-citrate at pH 8.0 by autoclaving for 1 h at 121 °C, and this procedure was repeated until no dark color was obtained (5 cycles of extraction). The sample was centrifuged at 10,000*g* for 20 min, the combined supernatant was filtered through Whatman No.1 paper, and analysed by the Bradford assay using bovine serum albumin as a standard. To determine GRSP-bound Al (Al-GRSP), a sample of GRSP was precipitated by slow addition of 2 M HCl to pH 2.0 and centrifuged at 8000*g* for 20 min. The pellet was redissolved in 0.5 M NaOH, dialyzed against deionized H_2O, and freeze-dried. Dried GRSP was mineralized by acid-digestion in $H_2O/HCl/HNO_3$(8/1/1 v/v/v) and Al was determined by atomic absorption spectroscopy (AAS).

2.3. Experimental design and data analysis

The experiment was established as a fully randomized factorial design, with six wheat cultivars and two lime treatments with 10 replicate pots containing three plants each for all treatment combinations; five pots were harvested each at 60 and 150 DAS.

Data were evaluated for normality and were log transformed as necessary. Colonization data were arcsine transformed. Response variables were analyzed using analyses of variance (ANOVA) followed by Tukey's LSD to identify significant differences among treatment means. Harvests were analyzed separately. Principal

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